



**QUEEN'S
UNIVERSITY
BELFAST**

Biological control agent selection under environmental change using functional responses, abundances and fecundities; the Relative Control Potential (RCP) metric

Cuthbert, R. N., Dick, J. T. A., Callaghan, A., & Dickey, J. W. E. (2018). Biological control agent selection under environmental change using functional responses, abundances and fecundities; the Relative Control Potential (RCP) metric. *Biological Control*, 121, 50-57. <https://doi.org/10.1016/j.biocontrol.2018.02.008>

Published in:
Biological Control

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

Copyright 2018 Elsevier.

This manuscript is distributed under a Creative Commons Attribution-NonCommercial-NoDerivs License (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Biological control agent selection under environmental change using
functional responses, abundances and fecundities; the Relative
Control Potential (RCP) metric

Ross N. Cuthbert^{a,b}, Jaimie T.A. Dick^a, Amanda Callaghan^b and James W.E. Dickey^a

^aInstitute for Global Food Security, School of Biological Sciences, Queen's University
Belfast, Medical Biology Centre, Belfast, BT9 7BL, Northern Ireland

^bEnvironmental and Evolutionary Biology, School of Biological Sciences, University of
Reading, Harborne Building, Reading, RG6 6AS, England

Corresponding author: Ross N. Cuthbert (rcuthbert03@qub.ac.uk)

ABSTRACT

We currently lack the capacity to rapidly and reliably predict the efficacy of biological control agents due to inadequate consistency in derivations of functional and numerical responses and potential effects of context-dependencies. Here, we propose and apply a novel metric, Relative Control Potential (RCP), which combines the functional response (FR, *per capita* effect) with proxies for the numerical response (NR, agent population response) to compare agent efficacies, where $RCP = FR \times \text{abundance}$ (or other proxies e.g. fecundity). The RCP metric is a comparative ratio between potential biocontrol agents, where values > 1 indicate higher relative control efficacy. Further, RCP can compare the efficacy of agents under environmental contexts, such as temperature change. We thus derived the RCP for two predatory cyclopoid copepods, *Macrocyclus albidus* (Cyclopoida: Cyclopidae) and *Megacyclus viridis* (Cyclopoida: Cyclopidae), towards larvae of the mosquito *Culex pipiens* (Diptera: Culicidae) under temperatures representative of current and future climate. Both copepods exhibited potentially population destabilising Type II FRs, with increasing temperatures inducing greater magnitude FRs through increased attack rates and decreased handling times. Attack rates by *M. albidus* were higher than *M. viridis*, yet handling times and maximum feeding rates were similar between the species across all temperatures. The inclusion of abundance data drives an elevated RCP of *M. albidus* and the integration of fecundity drives greater RCP of *M. albidus* at peak temperatures. Q_{10} values are indicative of increased feeding activity by both copepods with temperature increases, however relative feeding level increases of *M. viridis* slowed towards the peak temperature. We present RCP calculations and biplots that represent the comparative efficacies of the two biological control agents across temperatures. The Relative Control Potential (RCP) metric thus provides a new tool for practitioners to better assess the potential efficacy of biocontrol agents before their integration into management approaches for pests, vectors and invasive species.

Keywords: Functional response; Numerical response; Relative Control Potential; *Culex pipiens*; *Macrocyclus albidus*; *Megacyclus viridis*

1. Introduction

Biological control has been applied to manage pests, vectors and invasive species in a variety of ecological systems (O’Neil, 1990; Marten and Reid, 2007; Van Driesche and Bellows, 2011; Calvo et al. 2016). However, attempts to reveal agent efficacy through the coupling of functional and numerical responses (FRs, NRs) are limited in practice, reducing our predictive capacity for population-level effects (but see Heisswolf et al. 2009; Costa et al. 2017). Further, natural systems are characterised by a number of abiotic and biotic context-dependencies that can alter species interaction strengths, including structural complexity (Barrios-O’Neill et al. 2015), temperature (Wasserman et al. 2016; South et al. 2017), dissolved oxygen (Lavery et al. 2015), parasitism (Bunke et al. 2015; Lavery et al. 2017a) and multiple/higher predators (Alexander et al. 2013; Barrios-O’Neill et al. 2014). Thus, rapid and reliable FR and NR derivations under context-dependencies are critical for the future of biocontrol strategies.

Effects associated with environmental change can be particularly profound in modulating natural systems. Indeed, climate change, coupled with urbanisation, is stimulating an unprecedented change in the population dynamics and status of mosquito vectors and their transmission of disease (Townroe and Callaghan, 2014; Medlock and Leach, 2015; Siraj et al. 2017), with mosquito invasions increasing with the transportation of goods and humans (e.g. Yee, 2016; Medlock et al. 2017). The *Culex pipiens* (Diptera: Culicidae; Linnaeus, 1758) complex is widespread globally and act as one of the primary vectors of West Nile virus in the USA and continental Europe (Hubalek and Halouzka, 1999; Fonseca et al. 2004).

Freshwater cyclopoid copepods exhibit marked potential for the biological control of mosquitoes (Marten and Reid, 2007; Baldacchino et al. 2017), and have been operationalised in large-scale field applications (Kay and Nam, 2005). However, we require rapid assessment of the relative biocontrol potential of such agents under changing climatic conditions. In this study, we therefore present and apply a new metric, based on FRs and NRs, to compare the efficacy of two native and widely-distributed copepods, *Macrocyclops albidus* (Cyclopoida: Cyclopidae; Jurine, 1820) and *Megacyclops viridis* (Cyclopoida: Cyclopidae; Jurine, 1820) under current and predicted temperature regimes.

Functional responses (FRs) quantify consumption under differing resource densities, describing the key components of search, capture and handling time. Three broad FR types have been described: the linear Type I, hyperbolic Type II and sigmoidal Type III (Solomon, 1949; Holling, 1959). Functional response form and magnitude are both powerful predictors of the impacts of consumers on resource populations across taxonomic and trophic groups (Dick et al. 2014; 2017). However, as FRs only assess *per capita* impacts, incorporation of the Numerical Response (NR), that is the consumer population response, is also required to discern the Total Response (TR) of consumers, whereby:

$$TR = FR \times NR$$

(1)

In comparison to FRs, NRs are inherently more nebulous and difficult to quantify (Dick et al. 2017). Thus, simple consumer abundance (AB) has recently been proposed as a proxy for the numerical response, giving the ‘Impact Potential’ (IP) metric, which has proved robust in predicting ecological impact in the context of invasion biology (Dick et al. 2017; Lavery et al. 2017b):

$$IP = FR \times AB$$

94 (2)

95 where FR is the maximum feeding rate (reciprocal of handling time) and AB is a measure of
 96 consumer field abundance. In the context of biocontrol, we can express this as ‘Control
 97 Potential’, CP:

$$98 \quad CP = FR \times AB$$

99 (3)

100 where FR is the maximum feeding rate as above. However, in addition, we propose that
 101 attack rate be used as a second measure of FR. The attack rate parameter describes the slope
 102 of the FR curve at low prey densities and high attack rates can thus be particularly
 103 destabilising to prey populations. CP as an absolute measure is, however, rather meaningless,
 104 and needs a comparator. Thus, where two or more biocontrol agents require assessment as to
 105 their relative potential efficacies, CP can become ‘Relative Control Potential’ (RCP):

$$106 \quad RCP = \left(\frac{FR_{\text{agent A}}}{FR_{\text{agent B}}} \right) \times \left(\frac{AB_{\text{agent A}}}{AB_{\text{agent B}}} \right)$$

107 (4)

108 where $RCP = 1$, we predict no difference between biocontrol agents; for $RCP < 1$, we predict
 109 agent A to have lesser efficacy than agent B; whereas when $RCP > 1$, agent A is predicted to
 110 have greater efficacy than agent B. Further, increasing values above 1 indicate increasing
 111 relative efficacy of agent A compared to agent B.

112 Furthermore, we propose the use of fecundity as a second proxy for NR, which
 113 enables the incorporation into RCP of how quickly biocontrol agents can proliferate. Error
 114 can also be incorporated into the RCP metric depending on data availability, using a
 115 probability density function (pdf) to generate confidence intervals (CIs) and probabilities that
 116 $RCP > 1$ or > 10 (see Dick et al. 2017). Moreover, as environmental gradients such as

temperature can have profound impacts on consumer-resource interactions (Englund et al. 2011; Rall et al. 2012), RCP can be used to compare the efficacy of each biocontrol agent across environmental gradients. Here, we apply the RCP metric (Eqn. 4) to compare the biological control potentials of the copepods *M. albidus* and *M. viridis* towards the mosquito complex *C. pipiens* over a temperature gradient reflective of current and future UK climate change scenarios. We also apply the Q_{10} coefficient to further illustrate feeding activity responses of the two agents across temperatures (Bennett, 1990).

2. Materials and methods

2.1. Animal collection and rearing

M. albidus and *M. viridis* were collected at Glastry Clay Pit Ponds, Northern Ireland (54°29'18.5"N; 5°28'19.9"W) in January 2017 and kept in Queen's Marine Laboratory, Portaferry, N. Ireland, at 25 ± 2 °C under a 16:8 light:dark regime and 50 – 60% relative humidity, since these conditions stimulated proliferation. Cultures were initiated using ovigerous females, placed individually into 250 mL cups with dechlorinated tap water and fed *ad libitum* with *Chilomonas paramecium* and *Paramecium caudatum* to obtain nauplii. Starter cultures of these protozoans were available commercially (Sciento, Manchester, England) and cultured under the same laboratory conditions in 2 L glass beakers using autoclaved wheat seeds, with *C. paramecium* providing nourishment for nauplii and early copepodids and *P. caudatum* for late copepodids and adults. Adult copepods were identified by Maria Holyńska, Museum and Institute of Zoology, Warsaw, Poland. Copepods were mass-reared in 10 L tanks and fed *ad libitum* on the protozoan diet. At maturity, copepods were maintained at 12 ± 2 °C under a 12:12 light and dark regime and acclimatised for 7 d

prior to experimentation in 5 L holding arenas of 22 cm diameter fed *ad libitum* on the protozoan prey.

Culex pipiens were obtained from a laboratory colony established at the University of Reading, England several years prior, originating from field-collected mosquitoes at the Pirbright Institute, Surrey, England. The colony was sustained under the same conditions as the copepod cultures, at 25 ± 2 °C in $32.5 \times 32.5 \times 32.5$ cm cages (Bugdorm, Watkins and Doncaster, Leominster, England) and fed three times per week with defibrinated horse blood (TCS Biosciences, Buckingham, England) using a Hemotek® blood-feeding system (Hemotek Ltd., Accrington, England) and additionally provided with cotton pads soaked in a 10% sucrose solution. Cages contained black cups filled with 200 mL dechlorinated tap water for oviposition. Egg rafts were extracted three times per week and placed into larval bowls containing 3 L dechlorinated tap water, and fed *ad libitum* with ground guinea pig pellets (Pets at Home, Newtownabbey, Northern Ireland) until pupation.

2.2. Experimental procedure

Non-ovigerous adult female *M. albidus* and *M. viridis* (1.6 – 1.8 mm and 2.0 – 2.3 mm body length excluding caudal setae, respectively) were selected for experiments. We selected non-ovigerous females to standardise predators as cyclopoids are sexually dimorphic (Laybourn-Parry et al. 1988) and to eliminate cannibalism of hatching juveniles (Toscano et al. 2016). First instar *C. pipiens* larvae (1.1 – 1.3 mm) were used as prey. Functional response experiments were undertaken in transparent polypropylene cups (42 mm dia.) containing 20 mL dechlorinated tap water from a continuously aerated source in a 12:12 light and dark regime over 24 h at temperatures representing reasonable current autumn/winter (12 °C), spring/summer (16 °C) and future spring/summer (20 °C) conditions in the UK (± 0.1 °C; Clifton NEIB water baths; Hulme et al. 2002; Hammond and Pryce, 2007). Dissolved oxygen

was monitored using a YSI model 550A meter (Letchworth, England) to ensure levels remained above 80% saturation. Both predators and prey were acclimatised to the two elevated temperatures over a two hour period prior to experiments; temperatures were increased every 30 minutes by either 1 °C or 2 °C (i.e. to 16 °C or 20 °C). Following the acclimatisation period, we added single adult females of either *M. albidus* or *M. viridis* to containers with prey densities of 2, 4, 8, 15, 30 and 60 ($n = 4$ per experimental group). Controls consisted of four replicates at each prey density and temperature in the absence of predators. Predators were individually starved for 24 h in containers of the same volume and diameter as the experimental arenas before being transferred to containers holding the corresponding prey density. Predators were removed from experimental arenas after 24 hours, with the numbers of prey alive counted to derive the numbers killed in each replicate.

2.3. Data manipulation and statistical analyses

Statistical analyses were undertaken in R v3.3.1. (R Core Team, 2016). Logistic regression of proportion of prey killed as a function of prey density was used to infer FR types; Type II FRs are characterised by a significant negative first-order term and Type III FRs by a significant positive first order term followed by a significant negative second order term. To account for prey depletion, we fitted Rogers' random predator equation for conditions without prey replacement (Trexler et al. 1988; Juliano, 2001):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \quad (5)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the total experimental period. The Lambert W function was applied due to the implicit nature of the random predator equation (Bolker, 2008). Attack rates and maximum feeding rates ' $1/h$ ' were non-parametrically bootstrapped ($n = 30$) to

facilitate modelling of FR parameters with respect to ‘predator’ and ‘temperature’ factors and their interactions. Bootstrapped parameters were analysed using generalised linear models (GLMs) assuming a quasi-Poisson distribution. F -tests were used in a step-deletion process to compare deviance between models (Crawley, 2007). We applied Tukey’s HSD method to infer specific pairwise differences using the ‘multcomp’ package in R (Hothorn et al. 2008).

Benthic survey data for *M. albidus* and *M. viridis* (as *Acanthocyclops viridis*) derived from Tinson and Laybourn-Parry (1986) were used to calculate RCP based on maximum field abundances using pooled bootstrapped mean maximum feeding and attack rates across all three temperatures. To calculate RCP using fecundity, we used results from Laybourn-Parry et al. (1988) to discern the proportion of total consumed energy devoted to reproduction across corresponding temperatures for the two copepods:

$$\text{Fecundity} = \left(\frac{P_r}{C} \right) \times 100 \quad (6)$$

where P_r is the quantity of energy expended through the production of eggs and C is the total energy consumed at a given temperature (Table 1). Reproductive energy proportions at 16 °C were supplemented with those available for 15 °C. We generated ‘RCP biplots’ to present the RCP (see Lavery et al. 2017b) of the two predators using both the abundance (AB) and fecundity (FE) proxies for the numerical response.

We additionally calculated Q_{10} values to further quantify the effects of increased temperature on feeding rates and compare how these varied between predatory cyclopoids:

$$Q_{10} = \left(\frac{FR_2}{FR_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)} \quad (7)$$

where Q_{10} is a coefficient without units, FR_1 is the maximum feeding rate at temperature T_1 and FR_2 is the maximum feeding rate at temperature T_2 . The Q_{10} coefficient assesses how temperature increases of 10 °C affect the rate of biological processes (Bennett, 1990); values of 1 – 1.5 are associated with a thermal plateau and values of 2 – 4 indicate substantive increases in activity as temperature increases (Huey, 1982; Bennett, 1990).

3. Results

Prey survival in control treatments was a minimum of 98.5% across temperatures, and thus experimental deaths were attributed to predation by copepods, which was also directly observed. Type II FRs were found in all predator and temperature combinations, as indicated by significantly negative first order terms (Table 2; Figure 1). Overall, attack rates (initial FR slopes; see Figure 1) for *M. albidus* were significantly higher than for *M. viridis* ($F_{1, 178} = 7.25, p = 0.01$) and increased significantly with temperature ($F_{2, 176} = 74.41, p < 0.001$). There were significant increases in attack rates between 12 °C and 16 °C ($z = 5.61, p < 0.001$), and 12 °C and 20 °C ($z = 6.75, p < 0.001$), but not between 16 °C and 20 °C ($z = 1.20, p = 0.45$). There was a significant ‘predator × temperature’ interaction ($F_{2, 174} = 3.09, p = 0.05$), reflecting significantly greater attack rates by *M. albidus* only at 12 °C ($z = 3.42, p = 0.01$; Table 2; Figure 1). Overall, maximum feeding rates (asymptotes of FR curves; see Figure 1) did not differ significantly between the two predators ($F_{1, 178} = 2.88, p = 0.09$), but increased significantly with temperature ($F_{2, 176} = 110.29, p < 0.001$; Figure 1). There were significant increases in maximum feeding rates between all temperature levels (12 °C – 16 °C, $z = 4.23, p < 0.001$; 16 °C – 20 °C, $z = 4.79, p < 0.001$; 12 °C – 20 °C, $z = 8.81, p < 0.001$). There was a significant ‘predator × temperature’ interaction ($F_{2, 174} = 3.46, p = 0.03$), reflecting a non-significant difference between maximum feeding rates of *M. albidus* at 20 °C and *M. viridis*

at 16 °C ($z = 2.48$, $p = 0.13$), compared to a significantly lower maximum feeding rate of *M. albidus* at 16 °C in comparison to *M. viridis* at 20 °C ($z = 6.24$, $p < 0.001$).

The RCP calculations integrating field abundances with maximum feeding and attack rates are presented in Table 3. *M. albidus* displays much higher abundance than *M. viridis*, driving greater RCP using both FR parameters (Figure 2a and 2b). There is a general increase in the proportion of total consumed energy devoted to reproduction as temperature increases (Table 1). Anomalous to this is the response to warming of *M. viridis* at 20 °C, with fecundity here falling markedly (Table 1). There are relatively similar levels of RCP for the two species illustrated at both 12 °C and 16 °C, followed by a substantial decrease in efficacy of *M. viridis* at 20 °C (Table 4; Figures 2c and 2d). Indeed, the certainty of the RCP using fecundity strengthens at peak temperatures (Table 4). Under both NR proxies, differential efficacies between predators were more pronounced using the attack rate parameter (Figure 2). The Q_{10} coefficients for the two predators across the temperature gradient indicate that between 12 °C and 20 °C both the feeding rates of *M. albidus* and *M. viridis* were highly responsive to temperature increases. There was a marked difference between the predators in the incremental drivers of this response, with *M. viridis* exhibiting a rapid increase between 12 °C and 16 °C which slowed between 16 °C and 20 °C. Conversely, *M. albidus* was consistent in its feeding response to increased temperatures (Table 5).

4. Discussion

Biological control of pests, disease vectors and invasive species can be effective (e.g. Hajek, 2007; Nam et al. 2012; Veronesi et al. 2015), but efforts to predict the efficacy of natural enemies are limited when *per capita* effects (e.g. Functional Responses; FRs) are solely considered (Lester and Harmsen, 2002; Fernández-arhex and Corley, 2003). The

complementary agent population response (e.g. Numerical Response; NR) is, however, somewhat nebulous and more difficult to derive, with proxies for the NR required to allow rapid assessment of the overall impact of a consumer (i.e. Total Response; TR; Dick et al. 2017). Recent developments that combine functional and numerical responses (or their proxies) into the comparative Relative Impact Potential metric (RIP; Dick et al. 2017) yield high explanatory and predictive power for the ecological impacts of invasive species. Indeed, this RIP approach was 100% successful at identifying high impact invasive species, and the metric correlated tightly with degree of ecological impact (i.e. reduction of native species populations). Hence, the present RCP metric is promising to assess the efficacy of biocontrol agents, which are chosen on the same basis regarding impact on populations of target species (see Dick et al. 2017). Further value in the application of RCP surrounds the integration of context-dependencies associated with environmental change, which can strongly affect interactions between consumers and their resources (e.g. oxygen availability: Lavery et al. 2015; habitat complexity: Barrios-O'Neill et al. 2015). Thus, we present the new Relative Control Potential (RCP) metric that uses *per capita* and consumer population responses to compare efficacy among biocontrol agents and can allow predictions of changes in such efficacies under context-dependencies.

The risk of mosquito-borne disease at continental scales has reached unprecedented levels in recent decades (Medlock and Leach, 2015). Arboviruses such as Zika, West Nile, dengue and chikungunya present enormous public health concerns, with disease dynamics shifting rapidly under environmental change (Benelli and Mehlhorn, 2016; Siraj et al. 2017). Agricultural systems will additionally be impacted (Chevalier, 2013). This risk necessitates the formation of techniques to assess and compare the potential efficacies of biological control agents. Here, RCP revealed *M. albidus* as a more effective agent than *M. viridis*. Temperature was shown to mediate changes to the FR parameters of *M. albidus* and *M.*

viridis, driving higher magnitude FRs through increasing attack rates and decreasing handling times. The temperature-dependence of attack rates reported here contrasts to suggestions that this FR parameter is temperature-independent (Rall et al. 2012; Dell et al. 2014). We show that both predators exhibit high maximum feeding rates that exceed 30 of the West Nile virus vector *C. pipiens* per day at 20 °C. Critically, the Type II FRs found are indicative of a capacity to destabilise prey populations due to high proportional consumption at low prey densities (Long and Whitefleet-Smith, 2013). *M. albidus* and *M. viridis* show strong similarities in their *per capita* consumption, although the attack rates of *M. albidus* were significantly greater overall, illustrated by steeper gradients in the FR curves at low densities. As a result, *M. albidus* may be more effective in controlling *C. pipiens* populations.

We demonstrate that integrating field abundances with RCP reveals far stronger control efficacies of *M. albidus* compared to *M. viridis*. The utility of abundance estimates lies in the projection of how many conspecifics may engage in the predator-prey (or other consumer-resource) interaction and it is thus a useful NR proxy. On the other hand, incorporating measures of fecundity estimates how rapidly biological control agents can reproduce when introduced. Using fecundity, we demonstrate temperature-dependencies of control efficacy. Large fecundity variabilities are illustrated in the RCP biplots, with the reproductive allocation of *M. viridis* declining rapidly at 20 °C, whilst that of *M. albidus* continues to rise. The reduction in fecundity shown by *M. viridis* at 20 °C is concurrent with a slowing feeding activity response discerned through Q_{10} analysis, whereas *M. albidus* displays a consistent incremental increase in feeding with warming. Overall, *M. albidus* displays greater potential for the control of West Nile virus vector *C. pipiens* than *M. viridis*, particularly under climate change projections where our certainty for differential efficacy increases (e.g. Hulme et al. 2002). This differential efficacy is more pronounced when the attack rate parameter is considered. An increased metabolic demand could enable *M. albidus*

to sustain efficiency in the consumption of *C. pipiens*, which proliferate more rapidly at higher temperatures, particularly in domestic and peri-domestic habitats in urbanised environments (Townroe and Callaghan, 2014).

In this study, temperature had a profound effect on predator-prey interactions. It has been suggested that interaction strengths of ambush predators such as the benthic copepods examined here are temperature independent (Awasthi et al. 2012; Novich et al. 2014). Thus, marked thermal dependencies may result, rather, from individual prey foraging responses to temperature change, wherein motility and velocity may increase with warming. These interactions make predator-prey systems highly specific to both the species (Englund et al. 2011) and environment (Broitman et al. 2011), with optimal foraging patterns of ectothermic prey potentially peaking at intermediate temperatures (Englund et al. 2011; Kalinoski and DeLong 2016). Further, for endotherms, such interactions are often dependent on the specific feeding strategy (Dell et al. 2014). In this study, feeding rates of candidate biocontrol agents peaked at the highest temperature, however the rate of increase slowed between 16 °C and 20 °C, as compared to between 12 °C and 16 °C; this trend was particularly marked for *M. viridis*. Notably, these temperatures are well within the thermal tolerances of common cyclopoid copepods (Marten and Reid, 2007). Temperature additionally has a substantial influence on the development of the focal prey, *C. pipiens*, driving significant reductions in development times under conditions of warming (Loetti et al. 2011; Ruybal et al. 2016), and necessitating increased foraging intensity. Yet, increases in *C. pipiens* mortality due to drivers outside of predation are also evident as temperatures rise due to thermal stressors (Ruybal et al. 2016). *M. albidus* has been proved particularly effective against the invasive arbovirus vector *A. albopictus* following field trials (Marten, 1990; Veronesi et al. 2015). Previous research has suggested that copepods are more efficient consumers of *Aedes* spp. than *Culex* spp. as a result of morphological variations between the genera (Marten and Reid,

2007). However, laboratory trials have shown similar levels of overall predation by *M. albidus* towards both *A. albopictus* and *C. pipiens* (Veronesi et al. 2015), as well as by *Mesocyclops annulatus* (Micieli et al. 2002). Further field trials are required to elucidate whether their efficiencies towards *C. pipiens* translate empirically, particularly as it is the major West Nile virus vector in the USA and Europe (Hubalek and Halouzka, 1999; Fonseca et al. 2004) and part of one of the most widespread mosquito complexes in the world (Harbach, 2012).

In conclusion, this is the first study to develop and apply the new RCP metric to biological control agent selection. We demonstrate that the integration of abundance and fecundity estimations can provide a means to differentiate between biocontrol agents that display similar *per capita* efficacies across temperature gradients. We additionally illustrate the value in the use of maximum feeding and attack rates for instructing agent selection. Adaptations of this metric have been applied successfully in the context of invasion biology to explain and predict the ecological impact of invasive species (Dick et al. 2017; Lavery et al. 2017b), and similar fundamental principles enable its application to the selection of biocontrol agents. Overall, temperature increases will induce greater *per capita* predation pressure by predatory copepods towards *C. pipiens* and likely other mosquito species. Copepod applications to waterbodies can form an integral part of mosquito control efforts (Baldacchino et al. 2015), with large-scale field trials having proved successful (e.g. Kay and Nam, 2005), particularly given their ability to thrive in both natural and artificial waterbodies (Marten and Reid, 2007). Importantly, copepods can be augmented synergistically using existing control methods, such as the use of bacterial *Bacillus thuringiensis* var. *israelensis* (*Bti*; Kosiyachinda et al. 2003). Nanoparticles have additionally been found to heighten predation (Murugan et al. 2015). The straightforward derivation of the RCP metric, and its visual representation in biplots, will allow comparisons of biological control agents across

many ecological systems, and could increase cost-effectiveness of natural enemies in the long-term. Further proxies for the numerical response, such as biocontrol agent longevity or biomass, can be integrated into the RCP metric as per the requirements of the assessed system or biocontrol approach, increasing the robustness and flexibility of the method. Moreover, the additional integration of a qualifier to account for target organism responses under matched environmental change scenarios could bolster the power of the RCP metric in reliably selecting biocontrol agents, and this is worth further consideration in future research.

Authors' contributions

Relative Control Potential (RCP) concept and framework: RNC, JTAD and JWED. Design and execution of experimental trials: RNC and JTAD. Fitting functional response models and undertaking RCP calculations: RNC. First draft of the manuscript: RNC. Manuscript revisions: all authors.

Acknowledgements

Culex pipiens eggs were originally developed and supplied by The Pirbright Institute under BBSRC project code: BBS/E/I/00001701. This study was funded through, and forms part of, a PhD studentship provided by the Department for the Economy, Northern Ireland. We thank two anonymous reviewers for helpful comments.

References

[Alexander, M.E., Dick, J.T.A., O'Connor, N.E., 2013. Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos* 122\(11\), 1521–](#)

- 381 [1531.](#)
- 382 Awasthi, A.K., Wu, C-W., Tsai, K-H., King, C-C., Hwang, J-S., 2012. How does the ambush
383 predatory copepod *Megacyclops formosanus* (Harada, 1931) capture mosquito larvae of
384 *Aedes aegypti*? Zool. Stud. 51(7), 927–936.
- 385 [Baldacchino, F., Caputo, B., Chandre, F., Drago, A., della Torre, A., Montarsi, F., Rizzoli,](#)
386 [A., 2015. Control methods against invasive *Aedes* mosquitoes in Europe: A review. Pest](#)
387 [Manage. Sci. 71\(11\), 1471–1485.](#)
- 388 [Baldacchino, F. Bruno, M.C., Visentin, P., Blondel, K., Arnolid, D., Hauffe, H.C., Rizzoli,](#)
389 [A., 2017. Predation efficiency of copepods against the new invasive mosquito species](#)
390 [Aedes koreicus \(Diptera: Culicidae\) in Italy. Eur. Zool. J. 84\(1\), 43–48.](#)
- 391 [Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H.J., Alexander,](#)
392 [M.E., Bovy, H.C., 2014. Fortune favours the bold: A higher predator reduces the impact](#)
393 [of a native but not an invasive intermediate predator. J. Anim. Ecol. 83\(3\), 693–701.](#)
- 394 [Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H., 2015.](#)
395 [Predator-free space, functional responses and biological invasions. Funct. Ecol. 29\(3\),](#)
396 [377–384.](#)
- 397 [Benelli, G., Mehlhorn, H., 2016. Declining malaria, rising of dengue and Zika virus: insights](#)
398 [for mosquito vector control. Parasitol. Res. 115\(5\), 1747-1754.](#)
- 399 Bennett, A.F., 1990. Thermal dependence of locomotor capacity. Am. J. Physiol. 259(2),
400 253–258.
- 401 Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press, Princeton.
- 402 [Broitman, B.R., Szathmary, P.L., Mislán, K.A.S., Blanchette, C.A., Helmuth, B., 2009.](#)
403 [Predator-prey interactions under climate change: the importance of habitat vs body](#)

- 404 [temperature. Oikos 118\(2\), 219–224.](#)
- 405 [Bunke, M., Alexander, M.E., Dick, J.T.A., Hatcher, M.J., Paterson, R., Dunn, A.M., 2015.](#)
- 406 [Eaten alive: cannibalism is enhanced by parasites. Open Sci. 2, 140369.](#)
- 407 [Calvo, F.J., Torres-Ruiz., A., Velázquez-González, J.C., Rodríguez-Leyva, E., Lomeli-Flores,](#)
- 408 [J.R., 2016. Evaluation of *Dicyphus hesperus* for biological control of sweet potato](#)
- 409 [whitefly and potato psyllid on greenhouse tomato. Biocontrol 61\(4\), 415-424.](#)
- 410 [Chevalier, V., 2013. Relevance of Rift Valley fever to public health in the European Union.](#)
- 411 [Clin. Microbiol. Infect. 19\(8\), 705-708.](#)
- 412 [Costa, J.F., Matos, C.H.C., de Oliveira, C.R.F., da Silva, T.G.F., Lima Neto, I.F.A., 2017.](#)
- 413 [Functional and numerical responses of *Stethorus tridens* Gordon \(Coleoptera:](#)
- 414 [Coccinellidae\) preying on *Tetranychus bastosi* Tuttle, Baker & Sales \(Acari:](#)
- 415 [Tetranychidae\) on physic nut \(*Jatropha curcas*\). Biol. Control 111, 1-5.](#)
- 416 [Crawley, M.J., 2007. The R book. John Wiley & Sons, Chichester.](#)
- 417 [Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperature dependence of trophic interactions](#)
- 418 [are driven by asymmetry of species responses and foraging strategy. J. Anim. Ecol.](#)
- 419 [83\(1\), 70–84.](#)
- 420 [Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B.,](#)
- 421 [Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth,](#)
- 422 [K.D., Richardson, D.M., 2014. Advancing impact prediction and hypothesis testing in](#)
- 423 [invasion ecology using a comparative functional response approach. Biol. Invasions](#)
- 424 [16\(4\), 735–753.](#)
- 425 [Dick, J.T.A., Lavery, C., Lennon, J.J., Barrios-O'Neill., D., Mensink, P.J., Britton, R.,](#)
- 426 [Médoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J.,](#)

- 427 [Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J.,](#)
 428 [Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk,](#)
 429 [M.R., Aldridge, D.C., Caffrey, J.M., 2017. Invader Relative Impact Potential: a new](#)
 430 [metric to understand and predict the ecological impacts of existing, emerging and future](#)
 431 [invasive alien species. J. Appl. Ecol. 54\(4\), 1259–1267.](#)
- 432 [Englund, G., Ohlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the](#)
 433 [functional response. Ecol. Lett. 14\(9\), 914–921.](#)
- 434 [Fernández-arhex, V., Corley, J.C., 2003. The functional response of parasitoids and its](#)
 435 [implications for biological control. Biocontrol Sci. Technol. 13\(4\), 403–413.](#)
- 436 [Fonseca, D.M., Keyghobadi, N., Malcolm, C.A., Mehmet, C., Schaffner, F., Mogi, M.,](#)
 437 [Fleischer, R.C., Wilkerson, R.C., 2004. Emerging vectors in the *Culex pipiens* complex.](#)
 438 [Sci. 303\(5663\), 1535–1538.](#)
- 439 [Hajek, A., 2007. Introduction of a fungus into North America for control of gypsy moth, in:](#)
 440 [Vincent, C., Goettel, M.S., Lazarovits, G. \(Eds.\) Biological control: a global perspective.](#)
 441 [CAB International, Wallingford, pp. 53–62.](#)
- 442 Hammond, D., Pryce, A.R., 2007. Climate change impacts and water temperature.
 443 Environment Agency Science Report SC060017/SR. Bristol.
- 444 [Harbach, R.E., 2012. *Culex pipiens*: Species versus species complex - taxonomic history and](#)
 445 [perspective. J. Am. Mosq. Control Assoc. 28\(4\), 10–23.](#)
- 446 [Heisswolf, A., Klemola, N., Ammunét, T., Klemola, T., 2009. Responses of generalist](#)
 447 [invertebrate predators to pupal densities of autumnal and winter moths under field](#)
 448 [conditions. Ecol. Entomol. 34\(6\), 709–717.](#)
- 449 [Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can.](#)

- 450 [Entomol. 91\(7\), 385–398.](#)
- 451 [Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric](#)
- 452 [models. Biom. J. 50\(3\), 346–363.](#)
- 453 [Hubalek, Z., Halouzka, J., 1999. West Nile fever - a remerging mosquito-borne viral disease](#)
- 454 [in Europe. Emerg. Infect. Dis. 5\(5\), 643–650.](#)
- 455 [Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles, in: Gans, C., Pough,](#)
- 456 [F.H. \(Eds.\), Biology of the Reptilia. Academic Press, New York, pp. 25–91.](#)
- 457 Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J.,
- 458 Murphy, J.M., Hassell, D., Boorman, P., McDonald, R., Hill, S., 2002. Climate change
- 459 scenarios for the United Kingdom. The UKCIP Scientific Report. Tyndall Centre for
- 460 Climate Change Research, School of Environmental Sciences, University of East
- 461 Anglia, Norwich.
- 462 [Juliano, S.A., 2001. Non-linear curve fitting: predation and functional response curves, in:](#)
- 463 [Scheiner, S.M., Gurevitch, J. \(Eds.\), Design and Analysis of Ecological Experiments.](#)
- 464 [Oxford University Press, Oxford, pp. 178–196.](#)
- 465 [Kalinowski, R.M., DeLong, J.P., 2016. Beyond body mass: how prey traits improve predictions](#)
- 466 [of functional response parameters. Oecologia 180\(2\), 543–550.](#)
- 467 [Kay, B.H., V.S. Nam., 2005. New strategy against *Aedes aegypti* in Vietnam. Lancet](#)
- 468 [365\(9459\), 613-617.](#)
- 469 Kosiyaichinda, P., Bhumiratana, A., Kittayapong, P., 2003. Enhancement of the efficacy of a
- 470 combination of *Mesocyclops aspericornis* and *Bacillus thuringiensis* var. *israelensis* by
- 471 community-based products in controlling *Aedes aegypti* larvae in Thailand. Amer. J.
- 472 Trop. Med. Hyg. 69(2), 206–212.

- 473 [Laverty C., Dick, J.T.A., Alexander, M.E., Lucy, F.E., 2015. Differential ecological impacts](#)
 474 [of invader and native predatory freshwater amphipods under environmental change are](#)
 475 [revealed by comparative functional responses. Biol. Invasions 17\(6\), 1761–1770.](#)
- 476 [Laverty, C., Brenner, D., McIlwaine, C., Lennon, J.J., Dick, J.T.A., Lucy, F.E., Christian,](#)
 477 [K.A., 2017a. Temperature rise and parasitic infection interact to increase the impact of](#)
 478 [an invasive species. Int. J. Parasitol. 47\(5\), 291–296.](#)
- 479 [Laverty, C., Green, K.D., Dick, J.T.A., Barrios-O'Neill, D., Mensink, P.J., Médoc, V.,](#)
 480 [Spataro, T., Caffrey, J.M., Lucy, F.E., Boets, P., Britton, J.R., Pegg, J., Callagher, C.,](#)
 481 [2017b. Assessing the ecological impacts of invasive species based on their functional](#)
 482 [responses and abundances. Biol. Invasions 19\(5\), 1653–1665.](#)
- 483 [Laybourn-Parry, J., Abdullahi, B.A., Tinson, S.V., 1988. Temperature-dependent energy](#)
 484 [partitioning in the benthic copepods *Acanthocyclops viridis* and *Macrocyclops albidus*.](#)
 485 [Can. J. Zool. 66\(12\), 2709–2713.](#)
- 486 [Lester, P.J., Harmsen, R., 2002. Functional and numerical responses do not always indicate](#)
 487 [the most effective predator for biological control: An analysis of two predators in a two-](#)
 488 [prey system. J. Appl. Ecol. 39\(3\), 455–468.](#)
- 489 [Loetti, V., Schweigmann, N., Burrion, N., 2011. Development rates, larval survivorship](#)
 490 [and wing length of *Culex pipiens* \(Diptera: Culicidae\) at constant temperatures. J. Nat.](#)
 491 [Hist. 45\(36-36\), 2207–2217.](#)
- 492 [Long, W.C., Whitefleet-Smith, L., 2013. Cannibalism in red king crab: habitat, ontogeny, and](#)
 493 [the predator functional response. J. Exp. Mar. Biol. Ecol. 449, 142–148.](#)
- 494 Marten, G.G., 1990. Elimination of *Aedes albopictus* from tire piles by introducing
 495 *Macrocyclops albidus* (Copepoda, Cyclopidae). J. Am. Mosq. Control Assoc. 6(4), 689–

693.

[Marten, G.G., Reid, J.W., 2007. Cyclopoid copepods. J. Am. Mosq. Control Assoc. 23\(2\), 65–92.](#)

[Medlock, J.M., Leach, S.A., 2015. Effect of climate change on vector-borne disease risk in the UK. Lancet Infect. Dis. 15\(6\), 721–730.](#)

[Medlock, J.M., Vaux, A.G.C., Cull, B., Schäffner, F., Gillingham, E., Pfluger, V., Leach, S., 2017. Detection of the invasive mosquito species *Aedes albopictus* in southern England. Lancet Infect. Dis. 17\(2\), 140.](#)

[Micieli, M.V., Marti, G., García, J.J., 2002. Laboratory evaluation of *Mesocyclops annulatus* \(Wierzejski, 1892\) \(Copepoda: Cyclopidea\) as a predator of container-breeding mosquitoes in Argentina. Mem. Inst. Oswaldo Cruz. 97\(6\), 835–838.](#)

[Murugan, K., Benelli, G., Panneerselvam, C., Subramaniam, J., Jeyalalitha, T., Dinesh, D., Nicoletti, M., Hwang, J.S., Suresh, U., Madhiyazhagan, P., 2015. *Cymbopogon citratus*-synthesized gold nanoparticles boost the predation efficiency of copepod *Mesocyclops aspericornis* against malaria and dengue mosquitoes. Exp. Parasitol. 153, 129–138.](#)

[Nam, V.S., Yen, N.T., Duc, H.M., Tu, T.C., Thang, V.T., Le, N.H., Le Loan, L., Huong, V.T.Q., Khanh, L.H.K., Trang, H.T.T., Lam, L.Z.Y., Kutcher, S.C., Aaskov, J.G., Jeffery, J.A.L., Ryan, P.A., Kay, B.H., 2012. Community-based control of *Aedes aegypti* by using *Mesocyclops* in Southern Vietnam. Am. J. Trop. Med. Hyg. 86\(5\), 850–859.](#)

[Novich, R.A., Erickson, E.K., Kalinoski, R.M., DeLong, J.P., 2014. The temperature independence of interaction strength in a sit-and-wait predator. Ecosphere 5\(10\), 1–19.](#)

O’Neil, R.J., 1990. Functional response of arthropod predators and its role in the biological control of insect pests in agricultural systems, in: Dunn, P.E., Baker, R.R. (Eds.) New

- 519 directions in biological control: alternatives for suppressing agricultural pests and
 520 diseases. Alan R. Liss, Inc., New York, pp. 83–96.
- 521 R Core Team, 2016. R: A language and environment for statistical computing. R Foundation
 522 for Statistical Computing, Vienna.
- 523 [Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O.,](#)
 524 [Petchey, O.L., 2012. Universal temperature and body-mass scaling of feeding rates.](#)
 525 [Philos. Trans. R. Soc. Lond., Series B Biol. Sci. 367\(1605\), 2923–2934.](#)
- 526 [Ruybal, J.E., Kramer, L.D., Kilpatrick, A.M., 2016. Geographic variation in the response of](#)
 527 [Culex pipiens life history traits to temperature. Parasit. Vectors 9\(116\), 1–9.](#)
- 528 [Siraj, A.S., Oidtman, R.J., Huber, J.H., Kraemer, M.U.G., Brady, O.J., Johansson, M.A.,](#)
 529 [Perkins, T.A., 2017. Temperature modulates dengue virus epidemic growth rates](#)
 530 [through its effects on reproduction numbers and generation intervals. PLOS Negl.](#)
 531 [Trop. Dis. 11\(7\), e0005797.](#)
- 532 Solomon, M.E., 1949. The natural control of animal populations. J. Anim. Ecol. 18, 1–35.
- 533 [South, J., Dick, J.T.A., McCard, M., Barrios-O'Neill, D., Anton, A., 2017. Predicting](#)
 534 [predatory impact of juvenile invasive lionfish \(*Pterois volitans*\) on a crustacean prey](#)
 535 [using functional response analysis: effects of temperature, habitat complexity and light](#)
 536 [regimes. Environ. Biol. Fish. 100\(10\), 1155–1165.](#)
- 537 [Tinson, S., Laybourn-Parry, J., 1986. The distribution and abundance of benthic cyclopoid](#)
 538 [copepods in Esthwaite Water, Cumbria. Hydrobiol. 131\(3\), 225–234.](#)
- 539 [Toscano, B.J., Rombado, B.R., Rudolf, V.H.W., 2016. Deadly competition and life-saving](#)
 540 [predation: the potential for alternative stable states in a stage-structured predator–prey](#)
 541 [system. Proc. R. Soc. B. 283, 20161546.](#)

- [Townroe, S., Callaghan, A., 2014. British container breeding mosquitoes: The impact of urbanisation and climate change on community composition and phenology. PLoS ONE 9\(4\), e95325.](#)
- [Trexler, J.C., McCulloch, C.E., Travis, J., 1988. How can the functional response best be determined? Oecologia 76\(2\), 206–214.](#)
- [Van Driesche, R., Bellows, T.S., 2011. Biological control. Springer, Berlin.](#)
- [Veronesi, R., Carrieri, M., Maccagnani, B., Maini, S., Bellini, R. 2015. *Macrocyclus albidus* \(Copepoda: Cyclopidae\) for the biocontrol of *Aedes albopictus* and *Culex pipiens* in Italy. J. Am. Mosq. Control Assoc. 31\(1\), 32–43.](#)
- [Wasserman, R.J., Alexander, M.E., Weyl, O.L.F., Barrios-O'Neill, D., Froneman, P.W., Dalu, T., 2016. Emergent effects of structural complexity and temperature on predator-prey interactions. Ecosphere 7\(2\), e01239.](#)
- [Yee, D.A., 2016. Thirty years of *Aedes albopictus* \(Diptera: Culicidae\) in America: An introduction to current perspectives and future challenges. J. Med. Entomol. 53\(5\), 989–991.](#)

564 **Tables**

565 Table 1

Species	Temperature (°C)	C (mJ)	P_r (mJ)	Fecundity (%)
<i>M. albidus</i>	12	31210	2355	7.55
<i>M. albidus</i>	16	26150	2907	11.12
<i>M. albidus</i>	20	29150	3691	12.66
<i>M. viridis</i>	12	34433	2851	8.28
<i>M. viridis</i>	16	25311	3020	11.93
<i>M. viridis</i>	20	24960	1671	6.70

566

567

568

569

570

571

572

573

574

575 Table 2

Species	Temperature (°C)	1 st order term	<i>p</i>	Attack rate (<i>a</i>)	<i>p</i>	Handling time (<i>h</i>)	<i>p</i>
<i>M. albidus</i>	12	-0.02	< 0.001	1.28	< 0.001	0.07	< 0.001
<i>M. albidus</i>	16	-0.03	< 0.001	1.92	< 0.001	0.04	< 0.001
<i>M. albidus</i>	20	-0.04	< 0.001	2.37	< 0.001	0.04	< 0.001
<i>M. viridis</i>	12	-0.03	< 0.001	0.95	< 0.001	0.07	< 0.001
<i>M. viridis</i>	16	-0.03	< 0.001	1.90	< 0.001	0.04	< 0.001
<i>M. viridis</i>	20	-0.04	< 0.001	2.19	< 0.001	0.03	< 0.001

576

577

578

579

580

581

582

583

584

585

586 Table 3

Agent A, agent B comparison	Mean FR parameter (\pm SD)	Mean abundance (ind. $\text{m}^{-2} \pm \text{SD}$)	RCP	CI $p_{\text{RCP}} > 1$ (%)
<i>M. albidus</i> , <i>M.</i> <i>viridis</i>	1/h: 22.80 (\pm 8.37), 24.41 (\pm 10.55)	6727 (\pm 1018.23), 562 (\pm 288.50)	16.77	6.79 – 23.78 99.97***
<i>M. albidus</i> , <i>M.</i> <i>viridis</i>	a: 1.98 (\pm 0.72), 1.77 (\pm 0.67)	6727 (\pm 1018.23), 562 (\pm 288.50)	19.34	8.18 – 27.35 99.99***

587

588

589

590

591

592

593

594

595

596

597

598

599

600 Table 4

Agent A, agent B comparison	Temperature (°C)	Mean FR parameter (\pm SD)	Fecundity (%)	RCP	CI $p_{\text{RCP}} > 1$ (%)
<i>M. albidus</i> , <i>M. viridis</i>	12	1/h: 15.88 (\pm 4.36), 13.99 (\pm 2.67)	7.55, 8.28	1.07	0.77 – 1.34 51.93
<i>M. albidus</i> , <i>M. viridis</i>	16	1/h: 22.12 (\pm 7.64), 25.98 (\pm 9.68)	11.12, 11.93	0.90	0.53 – 1.21 32.58
<i>M. albidus</i> , <i>M. viridis</i>	20	1/h: 30.42 (\pm 5.24), 33.25 (\pm 6.73)	12.66, 6.70	1.80	1.39 – 2.17 98.21*
<i>M. albidus</i> , <i>M. viridis</i>	12	α : 1.43 (\pm 0.52), 1.05 (\pm 0.34)	7.55, 8.28	1.37	0.82 – 1.83 66.71
<i>M. albidus</i> , <i>M. viridis</i>	16	α : 2.17 (\pm 0.51), 2.02 (\pm 0.39)	11.12, 11.93	1.04	0.77 – 1.28 49.04
<i>M. albidus</i> , <i>M. viridis</i>	20	α : 2.34 (\pm 0.75), 2.24 (\pm 0.54)	12.66, 6.70	2.09	1.39 – 2.69 95.34*

601

602

603

604

605

606 Table 5

Species	Temperature (°C)	Mean max. feeding rate (1/h)	Q_{10} value
<i>M. albidus</i>	12 – 20	15.88 – 30.42	2.25
<i>M. albidus</i>	12 – 16	15.88 - 22.12	2.29
<i>M. albidus</i>	16 – 20	22.12 – 30.42	2.22
<i>M. viridis</i>	12 – 20	13.99 – 33.25	2.95
<i>M. viridis</i>	12 – 16	13.99 – 25.98	4.70
<i>M. viridis</i>	16 – 20	25.98 – 33.25	1.85

607

608

609

610

611

612

613

614

615

616

617

618

619

620

621

Captions

Table 1. Fecundity (%) calculations, entailing proportion of total consumed energy (C) devoted to production of eggs (P_r) in adult female *M. albidus* and *M. viridis* across 12 °C, 16 °C and 20 °C. Data relating to energetics adapted from Laybourn-Parry et al. (1988; $n = 5$; Eqn. 6).

Table 2. Results of logistic regression to denote functional response type across all predator and temperature treatments, alongside the starting attack rate (a) and handling time (h) parameter estimates and associated p -values generated using the Rogers' random predator equation (Eqn. 5).

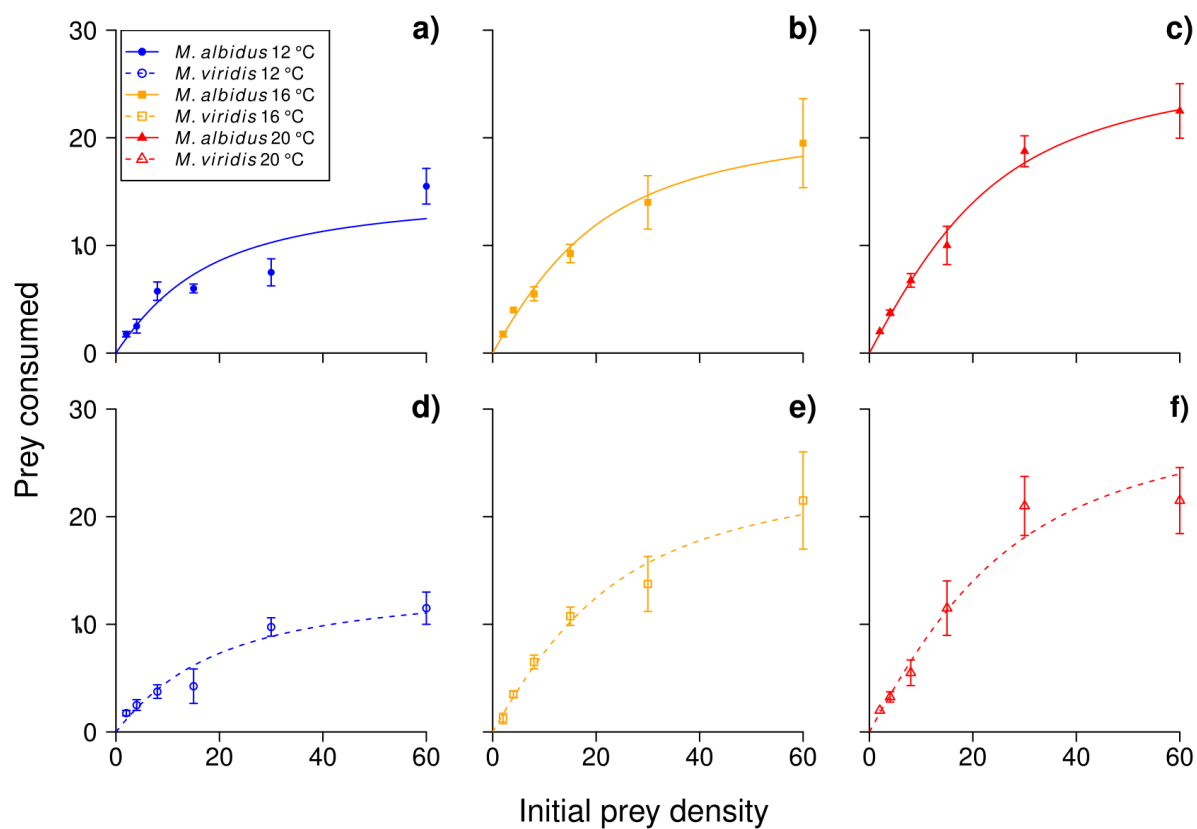
Table 3: Mean Relative Control Potential (RCP) using maximal abundances from Tinson and Laybourn-Parry (1986; $n = 8$) for *M. albidus* and *M. viridis*, alongside uncertainties reflected through 60% confidence intervals (CIs) and probability that the RCP output exceeds 1 using bootstrapped maximum feeding and attack rates. Asterisks denote significant levels of certainty that the RCP score is greater than 1 (* > 95%, ** > 99%, *** > 99.9%).

Table 4: Mean Relative Control Potential (RCP) using fecundities (%) across temperature change for *M. albidus* and *M. viridis* alongside uncertainties reflected through 60% confidence intervals (CIs) and probability that the RCP output exceeds 1 using bootstrapped maximum feeding and attack rates. Asterisks denote significant levels of certainty that the RCP score is greater than 1 (* > 95%, ** > 99%, *** > 99.9%).

Table 5: Q_{10} coefficient (Eqn. 7) values associated with mean bootstrapped maximum feeding rates for both predators between temperature gradients.

Figure 1. Functional responses of *M. albidus* (a, b, c) and *M. viridis* (d, e, f) towards first instar *C. pipiens* larvae at 12 °C (a, d), 16 °C (b, e) and 20 °C (c, f) over the 24 hour experimental period. Means are \pm SE at each prey density ($n = 4$).

Figure 2. RCP biplots comparing *M. albidus* and *M. viridis* using abundance estimates (a, b; $n = 8$) and fecundity calculations (c, d; Table 1), with FR parameters of maximum feeding (a, c) and attack rates (b, d). FR parameters in abundance biplots are pooled bootstrapped estimates across all temperatures ($n = 90$); those in fecundity plots are temperature-specific estimates ($n = 30$). Increasing CP is read from bottom left to top right. Abundance and FR parameter means are \pm SE.



665

666

667

668

669

670

671

672

673

